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ADMINISTRATIVE REPORT H-96-01

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Southwest Fisheries Science Center
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A Reevaluation of Shallow Reef Fish Populations at French Frigate Shoals and Midway Atoll in September 1995

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ABSTRACT

Divers conducted visual surveys of reef fishes at two sites, French Frigate Shoals (FFS) and Midway Atoll (MWAY), in September 1995. Surveys were repeated at the same stations at which fishes were surveyed in July 1992 (at FFS) and in August 1993 (MWAY), 12 and 13 years after they had been first surveyed in 1980. Nine stations in two habitats (four on inner and outer barrier reefs and five on lagoonal patch reefs) were surveyed at each of the two sites. Prior surveying protocols were repeated: divers counted all larger-than-recruit-sized ($\geq$ 2 cm Standard Length, SL) fish individuals, by species or lowest recognizable taxon, encountered within a band transect or other fixed area of reef. Another diver simultaneously estimated the body lengths of a random sample of fishes encountered within the same delimited area.

At FFS, the numerical densities of total fishes averaged 63% greater in September 1995 vs July 1992. The increases at FFS occurred in both major habitats, but were dominated by few taxa representing both herbivores and carnivores. Young-of-year (YOY) and other small-bodied ($\leq$ 7 cm SL) post-recruits represented about 47% of total fish counts at FFS in 1995 compared to 33% in 1992. Higher YOY counts in 1995 contributed in part to the numerical increase but influenced numbers more than they affected biomass estimates. Biomass densities were higher at FFS in 1995 vs 1992 because larger-bodied fish also were more numerous in 1995. Neither numerical densities, length frequency distributions, nor biomass densities meaningfully differed between 1995 and 1993 at MWAY. Patterns of numbers and biomass at MWAY and FFS are discussed relative to the possible current and future food limitation of Hawaiian monk seals, *Monachus schauinslandi*, at FFS.

INTRODUCTION

The Hawaiian monk seal, *Monachus schauinslandi*, is endemic to the Hawaiian Archipelago, where its present distribution in the Northwestern Hawaiian Islands (NWHI) is restricted to five main breeding populations, including French Frigate Shoals (FFS; 24°N, 166°W) and Midway Atoll (MWAY; 28°N, 177°W). Beginning in 1988 and continuing through 1995, the monk seal population at FFS, where about 30% of all NWHI monk seals currently reside, declined by 45-50%. These declines at FFS, particularly of juvenile seals, are thought to be related to decreases in the forage base of monk seals, whose broad diet consists of octopus, lobsters, and shallow-water demersal and reef fishes (DeLong et al., 1984; NMFS, unpubl. data).

In order to evaluate whether reef fish populations had recently declined from prior levels, shallow water reef fishes were surveyed at FFS and MWAY in the early nineties. Surveys were then repeated at stations previously surveyed by U.S. Fish & Wildlife personnel during 1980-83 (at FFS) and 1980 (MWAY). These repeat surveys were first conducted at FFS in July 1992 (DeMartini et al., 1993) and at MWAY in August 1993 (DeMartini et al., 1994). DeMartini et al. (1996, in press) provides a comprehensive interpretation of temporal comparisons at both sites. In general, the numerical densities of post-recruit-sized ($\geq$ 2 cm Standard Length, SL) reef fishes declined by about one-third between the early eighties and surveys made during the following decade. At least at MWAY, these declines included both herbivorous and carnivorous fishes and occurred in both major habitat types (DeMartini et al., 1996, in press). In this report, we update our shallow-water reef fish time series for surveys conducted at FFS and MWAY during September 1995.

METHODS AND MATERIALS

Field Surveys

FFS

Surveys were conducted over a 3-day period (September 13-15, 1995). Reef fishes were surveyed at historical ("test") stations using the same recording protocols as those used in July 1992, except that the estimates reported herein are based on data collected by two, rather than three, persons. As in July 1992, a total of four test stations on the barrier reef (BR: two Inner [Sta. Nos. 7, 8] and two Outer [Nos. 4, 6]), and five patch reef (PR) stations [Nos. 5c, 5d, 5e, 5f, 23] were surveyed. Each station was surveyed once; one diver (FAP) tallied densities on a 500 m^2 band transect (BR stations) or within a delimited area (PR stations), while a second diver (EED) simultaneously

characterized the body length distribution of fishes in the same station area. Fishes were tallied by species or lowest recognizable taxon. DeMartini et al. (1993) specifies recording protocols and DeMartini et al. (1996, in press) describes station locations and habitats.

MWAY

Surveys were conducted over 2 days (September 22-23, 1995). Reef fishes were surveyed at historical stations using recording protocols identical to those used in August 1993, except as noted above for FFS. A total of four test stations on the barrier reef (BR: two Inner [Nos. 14, 21] and two Outer [Nos. 10, 19]), plus five patch reef (PR) stations [Nos. 5, 6, 11, 17, 18] were resurveyed. DeMartini et al. (1994, 1996 in press) provides additional details.

Data Analyses

Species rankings were used to evaluate assemblage structure. Some species of parrotfishes (adult *Scarus* spp) and surgeonfishes (*Acanthurus* spp) that were at times difficult to distinguish underwater were pooled for analyses. Potential changes in numerical densities were evaluated for total fishes, herbivore and carnivore trophic levels, and each of four carnivore feeding guilds (benthic invertebrate-feeders or "benthic carnivores", corallivores, piscivores, and planktivores). Data limitations restricted analyses of size frequency distributions and biomass densities to total fishes and the two trophic levels. Data were post-classified into trophic levels and carnivore guilds as described by DeMartini et al. (1996, in press). Analyses focused on higher taxa for two principal reasons: (1) The existing data for fish in the monk seal diet has family and grosser taxonomic resolution; (2) The statistical power to detect changes $\geq$ 50% in NWHI reef fish densities using diver visual surveys is generally insufficient at the species level (power = [1-ß] < 0.80 at α_2 = 0.10; DeMartini et al., 1996, in press).

Temporal changes (1995 vs prior survey) in numerical densities were evaluated using bootstrapped paired-comparisons (Manly, 1991), with data paired by station between surveys. The results of 1,000 iterations were evaluated at α_2 = 0.10 (Manly, 1991), and Bonferroni's correction was used to control Type I error in multiple comparisons ($\alpha_{crit} = \alpha/m$, where m = number of comparisons; Manly, 1991, p. 52). Analogous comparisons of size-frequency distributions were made using 2-Sample Kolmogorov-Smirnov (K-S) tests (Siegel and Castellan, 1988). Biomass densities were calculated first for each taxon as the cross-product of mean body weight per fish and mean numerical density ($N \cdot 10\ m^{-2}$), and then summed over taxa. Variances were estimated by the delta method excluding covariances (Seber 1982, p. 9) because preliminary analyses indicated that covariances were trivial. Large-bodied transient predators (sharks and the two

jacks *Caranx ignobilis* and *C. melampygus*) were excluded from the biomass estimates.

Bootstrap comparisons were coded in Microsoft Quick Basic 4.5. All remaining analyses used PC SAS v. 6.03 (SAS 1988).

RESULTS

Relative Densities

FFS

Count data were log-normally distributed among species. The 10 most numerous species dominated total fish densities (78-80%, depending on habitat) during the September 1995 survey. The top 20 and top 30 taxa contributed 91-92% and 96-97% to total densities, depending on habitat. Within habitats, rankings among taxa were generally similar in 1992 and 1995 (Table 1).

MWAY

The 10 most numerous species dominated total densities (80-86%) in September 1995. The top 20 and top 30 taxa contributed 92-95% and 97-98% to total densities, depending on habitat. Rankings within habitat generally persisted between 1993 and 1995 (Table 2).

Numerical Densities

FFS

In September 1995, total fish densities averaged almost 20 individuals·10 m^{-2} overall, with herbivores and carnivores averaging 5.9 and 13.8 fish·10 m^{-2}, respectively (Tables 1, 3). Fishes were nearly fivefold denser overall on patch reefs, even though herbivores were somewhat more numerous on the barrier reef and carnivores more so on patch reefs (Tables 1, 3). The benthic carnivore guild dominated numerically in both habitats (46-66%; Tables 1, 3).

Bootstrapped paired-comparisons of densities for pooled (barrier and patch reef) habitats were significantly different (greater) in 1995 vs 1992 for total fishes (63%), total carnivores (90%), benthic carnivores (117%), piscivores (141%), and planktivores (51%; Table 3). Total fishes and herbivores changed (37% and 76% increases) on the barrier reef; detectable differences on patch reefs included total fishes (68%), total carnivores (107%), benthic carnivores (140%), piscivores (140%), and planktivores (58%; Table 3). The higher densities at FFS in September 1995 thus were spatially general although greater in magnitude at patch reefs.

The overall numerical increases at FFS were due to increases in relatively few species. With only about a half dozen taxa involved, increases were not apparent at the species level within major functional groups (Table 4). The largest contributors were a benthic carnivore (the goatfish *Mulloidichthys vanicolensis*), herbivorous juvenile parrotfishes, and two planktivores (the damselfishes *Dascyllus albisella* and *Chromis ovalis*). The major contributors thus represented both trophic levels and the two major carnivorous feeding guilds.

MWAY

Total densities averaged > 17 fish $10 \cdot m^{-2}$ overall in September 1995, with herbivores and carnivores averaging 4.6 and 12.8 fish$\cdot 10\ m^{-2}$, respectively (Tables 2, 5). Fishes were about 2.5-times denser overall on patch reefs, even though herbivores were relatively more abundant on the barrier reef, and carnivores were relatively more abundant on patch reefs (Tables 2, 5). The benthic carnivore guild dominated numerically in the two habitats (45-48%; Tables 2, 5).

Bootstrapped paired-comparisons differed insignificantly between 1995 and 1993 for total fishes, herbivores, pooled carnivores, and all but one carnivore guild in either major habitat (Table 5). The most suggestive apparent changes (total fishes: 42% and 31% increases on patch reefs and in both habitats pooled) were insignificant ($P = 0.32, 0.29$). Only a single change was detectable (for benthic carnivores: a 57% decrease on the barrier reef; Table 5).

Relatively few taxa contributed to the nominal increase in densities at MWAY (Tables 4,5). The greatest contributors to counts on patch reefs were *Chromis ovalis*, apogonid spp (juvenile cardinalfishes--another zooplanktivorous taxon), and two goatfish-benthic carnivores (*Parupeneus pleurostigma* and *Mulloidichthys flavolineatus*). The herbivorous manini (*Acanthurus triostegus*) was encountered in large numbers only at Inner BR stations; *Chromis ovalis* was generally abundant at both Inner and Outer BR stations (Table 5).

Length Frequency Composition

FFS

Relatively more young-of-year (YOY) and other small-bodied ($\leq$ 7 cm SL) fish contributed to the length frequency tallies of herbivores and carnivores (especially on the barrier reef) in September 1995 compared to July 1992 (2-sample K-S test, $P < 0.01$; Fig. 1A,B). Overall there were about 14% more (47 vs 33%) YOY-sized fishes tallied in September 1995 than in July 1992.

MWAY

Length frequency distributions for August 1993 and September 1995 were indistinguishable for herbivores and carnivores separately or for both trophic levels pooled in either major habitat (K-S tests, $P >> 0.10$; Fig. 2A, B).

Biomass

FFS

In September 1995, the biomass density of total fishes was 0.7-2.0 $kg \cdot 10\ m^{-2}$, with herbivores comprising 40-62% and carnivores 38-60%, depending on habitat. These 1995 estimates seem at least half again greater than the respective 1992 estimates for herbivores, carnivores and total fishes in either habitat (Fig. 3A). Variances are large (Fig. 3A), however, and statistical power is insufficient to resolve apparent increases to date. YOY-sized fishes contributed only about 1% and 2% to total biomass on the 1992 and 1995 surveys, respectively.

MWAY

Biomass densities in September 1995 averaged 0.9-2.1 $kg \cdot 10\ m^{-2}$, depending on habitat; about 32-65% were herbivores and 35-68% were carnivores. The respective estimates in August 1993 and September 1995 were similar except for herbivores on the barrier reef, for which several large-bodied or patchily abundant taxa (*Kyphosus* sp, *Scarus perspicillatus*, *Acanthurus triostegus*) disproportionately inflated both the magnitude of the biomass estimate and its variance in 1995 (Fig. 3B).

DISCUSSION

Temporal Comparisons of Relative Abundance

FFS and MWAY

The distributions of counts among taxa were fundamentally similar between the September 1995 and the July 1992 (FFS) or August 1993 (MWAY) surveys. We reasonably interpret this as indicating stability in assemblage structure. At FFS, despite quantitative changes in the abundance and size structure of reef fishes (see below), overall rank composition of the fish assemblage remained consistent. At MWAY, taxonomic rankings persisted along with estimated densities and size distributions.

Temporal Changes in Numerical Density

FFS

Between July 1992 and September 1995, the numerical densities of shallow reef fishes increased > 60%. These

increases were spatially general (an estimated 37% on the barrier reef and 63% on patch reefs), an indication that numerical increases had occurred (or were continuing to occur) on larger-than-physiographic spatial scales (Sale et al. 1994). Analogous mixtures of temporal change and spatial persistence at the level of individual coral reefs have recently been documented for shallow reef fishes elsewhere (Caley 1995).

MWAY

Unlike FFS, there was little suggestion that fish densities increased between 1993 and 1995 in either habitat. The strongest suggestion (a nominal 42% increase in total fish densities on patch reefs) was insignificant due to low statistical power. Most nominal changes at MWAY were small relative to those observed at FFS, regardless of power.

General

Caley (1995) recently documented latitudinal differences in reef fish dynamics between Lizard Island and One Tree Island on the Australian Great Barrier Reef that are perhaps analogous to those observed at FFS and MWAY. It may be unrealistic to expect the dynamics of reef fishes to track one another in regionally separated populations. Additional case studies are needed.

Temporal Patterns of Size Composition and Biomass

FFS

YOY-sized fishes were relatively more numerous at FFS in September 1995 compared to July 1992. The relative increase in YOY numbers between the two surveys (42%; as 47%-33% = 14/33 of total fishes tallied in 1995 and 1992, respectively) was substantial. Although the increase in YOY counts was less than that necessary to explain the observed increase of > 60% in total fish density, the higher YOY counts in part contributed to the general increase in numbers.

We do not believe it is likely that the 2-month difference in timing of the 1992 (July) and 1995 (September) surveys caused us to overestimate YOY in 1995. Most Hawaiian reef fishes have several-month-long egg and larval stages during protracted spawning seasons that peak in spring (Walsh 1987). If a bias was introduced by surveying in September instead of July, it should have been negative as a result of a longer period of attrition following the average time of peak recruitment in midsummer (Schroeder 1989).

The numerical increase in YOY contributed little to the recent increase in biomass densities at FFS. The higher apparent biomass densities in 1995 were primarily due to the greater numerical densities of larger-bodied fish. The latter may

represent the grow-out of juveniles from successful year classes that have become established since 1992. If so, it would signal the beginning of a cyclic upturn in productivity following the downturn that occurred during the late eighties-early nineties (Polovina et al. 1994, 1995).

MWAY

The relative abundances of YOY-sized fish were indistinguishable between September 1995 and August 1993, averaging about 31-33% of all fishes tallied. The potentially confounding effect of interannual differences in sampling times is even less likely at MWAY than at FFS because the difference in timing of the two surveys was less than a month.

Estimated biomass densities for herbivores on the barrier reef at MWAY were particularly imprecise because several taxa were by chance encountered in large, roving feeding schools that should not be considered spatially representative. The barrier reef herbivore data thus provide poor evidence for a recent major increase in standing biomass at MWAY. Rather, the biomass estimates for carnivores (and for herbivores on patch reefs) argue for little change between the 1993 and 1995 surveys.

General

We continue to estimate fish biomass densities on shallow NWHI reefs at levels of 1 kg·10 m^{-2} or greater. As noted by DeMartini et al. (1996 in press), such values are about twice the average level of fish standing biomass on shallow reefs in the Main Hawaiian Islands (MHI) (e.g., see Grigg 1994). We re-emphasize the importance of these differences as evidence for the high present and continuing level of exploitation of reef fishes in the MHI.

SUMMARY AND CONCLUSIONS

In September 1995, the numerical densities of reef fishes (all taxa, both major habitats) at FFS were 63% greater than they were when last surveyed in July 1992. Relatively greater increases were evident for herbivores, total carnivores, and benthic carnivores. The apparent September 1995 increases in total fishes at MWAY were nominal only. Length frequency distributions were skewed towards greater proportions of YOY-sized fishes in both major habitats at FFS on the 1995 survey, when their average was 42% greater than in 1992. YOY and other small-bodied fishes represented similar proportions (about 32%) of all fishes tallied at MWAY in 1995 and 1993. Only some of the recent increase in densities at FFS could be attributed to greater numbers of YOY. YOY contributed little (2%) to overall biomass densities at FFS in 1995. Biomass densities at FFS in 1995 appeared higher (0.7-2.0 kg·10 m^{-2}) than those estimated in

1992 (0.4-1.1 kg·10 m^{-2}) primarily because of the greater densities of larger-bodied fish. Biomass estimates at MWAY in 1995 (0.8 to < 2 kg·10 m^{-2}) were similar to those estimated in 1993 (1.0-1.1 kg·10 m^{-2}).

The increases in recruitment observed at FFS in September 1995 portend the continuation of recent reef fish increases, but these increases may have not yet fully translated to adult standing biomass. Subsequent surveys, over several or more years, would be necessary to document a continued establishment of year classes, and the subsequent elaboration of biomass through growth necessary for substantial increases in the reef fish forage base at FFS. Nominal increases in reef fishes at MWAY need further documentation because of the importance of this site for potential translocation of seals. In general, the link between reef fish recruitment and production and meaningful increases in the reef fish component of the monk seal forage base needs to be further described.

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Table 1.--FFS. Mean numerical densities ($N \cdot 10\ m^{-2}$) of major fish taxa on the July 1992 and September 1995 surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each survey for both habitat types pooled. Trophic guild acronyms are: bc = benthic carnivores; h = herbivores; co = corallivores; zp = planktivores; pi = piscivores. A dashed horizontal line separates the top 30, 1992 taxa from lower-ranked taxa that ranked within the top 30 on the 1995 survey.

	July 1992				September 1995			
Taxon	Rank92	DBR	DPR	Dboth	Rank95	DBR	DPR	Dboth
Thalassoma duperrey(bc)	1	.90	1.72	1.35	4	.74	1.52	1.18
Juvenile Scaridae(h)	2	.19	1.98	1.18	2	.64	3.53	2.25
Ctenochaetus strigosus(h)	3	.33	1.82	1.16	7	.63	1.24	.97
Dascyllus albisella(zp)	4	.06	2.02	1.15	3	abs	3.47	1.73
Stegastes fasciolatus(h)	5	.22	1.72	1.05	6	.10	1.75	1.02
Chaetodon miliaris(zp)	6	.03	1.74	.98	10	.06	.76	.45
Chromis vanderbilti(zp)	7	1.26	abs	.63	9	1.00	.01	.45
Acanthurus triostegus(h)	8	.33	.75	.56	11	.20	.61	.43
Mulloid. flavolineatus(bc)	9	abs	.84	.42	13	abs	.64	.32
Neoniphon sammara(bc)	10	abs	.59	.30	8	<.01	.96	.54
Zebrasoma flavescens(h)	11	.02	.45	.26	23	.04	.20	.13
Centropyge potteri(h)	12	.08	.36	.23	16	.08	.36	.24
Mulloid. vanicolensis(bc)	13	abs	.45	.22	1	abs	8.83	4.41
Canthigaster jactator(bc)	14	.12	.30	.22	21	>.08	.23	.16
Acanthurus spp[a](h)	15	.35	.08	.20	12	.73	.19	.43
Labroides phthirophagus(bc)	16	<.01	.35	.20	31	.03	.09	.07
Stethojulis balteata(bc)	17	.04	.25	.16	15	.17	.39	.29
Thalassoma ballieui(bc)	18	.12	.18	.15	20	.17	.21	.19
Paru. multifasciatus(bc)	19	.04	.23	.15	18	.10	.29	.21
Chromis hanui(zp)	20	.07	.21	.15	14	>.36	.25	.30
Scarus spp[b](h)	21	.05	.20	.13	17	.26	.19	.22
Bodianus bilunulatus(bc)	22	.06	.15	.11	29	.08	.07	.07
Chromis ovalis(zp)	23	.03	.17	<.11	5	.30	1.79	1.12
Gomphosus varius(bc)	24	<.01	.15	.09	43	.03	.05	.04
Chaetodon fremblii(bc)	25	.04	.12	.09	26	.03	.12	.08
Cheilinus unifasciatus(pi)	26	abs	.17	.09	25	abs	.15	.08
Synodontidae(pi)	27	<.01	.12	.07	52	abs	<.03	.01
Paru. pleurostigma(bc)	28	<.01	.11	.06	36	abs	.11	.05
Plectro. johnstonianus(co)	29	.02	.06	.04	30	.03	.11	.07

Table 1.--FFS (continued).

Taxon	July 1992				September 1995			
	Rank92	DBR	DPR	Dboth	Rank95	DBR	DPR	Dboth
Epibulus insidiator(pi)	30	<.01	.07	.04	35	.01	.09	<.06
Lutjanus kasmira(bc)	61	abs	<.01	<.01	19	abs	.41	.21
Macrophar. geoffroy(bc)	32	>.01	.06	.04	22	<.02	.27	>.15
Naso unicornis(h)	33	.01	.06	.04	24	>.02	.19	>.11
Naso lituratus(h)	49	<.01	<.01	<.01	27	>.02	.12	.08
Aulostomus chinensis(pi)	39	abs	.04	.02	28	abs	.15	.07
Top 10 taxa		3.9	13.6	8.8		5.0	24.5	14.1
Top 20 taxa		4.4	16.3	10.7		5.9	27.7	16.9
Top 30 taxa		4.6	17.4	11.6		6.2	29.1	18.0
Total fishes		4.7	18.1	12.1		6.4	30.4	19.7

[a/] *Acanthurus nigroris, A. nigrofuscus, A. blochii, A. xanthopterus, A. dussumieri, and A. olivaceus*

[b/] *Scarus* spp adults, including *S. perspicillatus* and *S. sordidus*

Table 2.--MWAY. Mean numerical densities ($N \cdot 10\ m^{-2}$) of major fish taxa on the August 1993 and September 1995 surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each sampling period for both habitat types pooled. For trophic guild acronyms see Table 1 caption. A dashed horizontal line separates the top 30, 1993 taxa from lower-ranked taxa that ranked within the top 30 on the 1995 survey.

	August 1993				September 1995			
Taxon	Rank93	DBR	DPR	Dboth	Rank95	DBR	DPR	Dboth
Stegastes fasciolatus(h)	1	2.10	2.67	2.42	2	1.34	1.88	1.64
Dascyllus albisella(zp)	2	abs	3.75	1.88	6	abs	2.62	1.31
Thalassoma duperrey(bc)	3	2.37	1.15	1.70	8	>.64	1.15	.93
Paru. pleurostigma(bc)	4	<.01	1.27	.71	4	abs	2.84	1.42
Juvenile Scaridae(h)	5	<.04	1.20	.68	10	<.02	1.12	.63
Chromis ovalis(zp)	6	.27	.59	.45	3	1.54	1.52	1.53
Thalassoma ballieui(bc)	7	.38	.47	.43	11	>.34	.23	.28
Coris venusta(bc)	8	.04	.63	.37	14	.04	.40	.24
Chaetodon miliaris(zp)	9	<.01	.55	.31	9	<.02	1.50	.84
Stethojulis balteata(bc)	10	.36	.24	.29	20	.17	.16	.17
Acanthurus spp[a](h)	11	.28	.29	.28	15	>.44	abs	.22
Kyphosus sp(h)	12	.56	.02	.26	13	.52	abs	.26
Bodianus bilunulatus(bc)	13	.07	.34	.22	34	.07	>.02	.04
Apogon spp(zp)	14	<.01	.38	.21	1	abs	3.73	1.86
Abudefduf abdominalis(zp)	15	.42	.04	.21	16	.08	.34	.22
Calotomus sp(h)	16	abs	.42	.21	39	<.01	.06	<.04
Scarus spp[b](h)	17	>.12	.22	.18	18	<.28	>.12	.19
Ctenochaetus strigosus(h)	18	.18	.16	.17	24	.09	>.11	.10
Plectro. johnstonianus(co)	19	.25	.09	.16	29	>.06	<.09	.08
Chaetodon fremblii(bc)	20	.03	.26	.16	19	.02	.32	>.18
Anampses cuvier(bc)	21	.12	.17	.15	40	.05	>.02	<.04
Acanthurus leucopareius(h)	22	.28	abs	.14	27	<.18	abs	.09
Cheilinus bimaculatus(bc)	23	abs	.27	.13	17	abs	.43	<.22
Paracirrhites forsteri(bc)	24	abs	.23	.12	30	abs	.11	.06
Labroides phthirophagus(bc)	25	.06	.16	.11	43	.03	.03	.03
Canthigaster jactator(bc)	26	.03	.18	.11	21	.01	.27	.16
Acanthurus triostegus(h)	27	.17	abs	.08	5	2.84	.21	1.38
Cirrhitops fasciatus(bc)	28	.02	.10	.07	65	<.01	abs	<.01
Mulloid. vanicolensis(bc)	29	.13	abs	.06	--	abs	abs	abs
Paru. porphyreus(bc)	30	.02	.09	.06	12	abs	.54	.27

Table 2.--MWAY (continued).

Taxon	August 1993				September 1995			
	Rank93	DBR	DPR	Dboth	Rank95	DBR	DPR	Dboth
Mulloid. flavolineatus(bc)	60	<.01	abs	<.01	7	.04	2.14	1.21
Myripristis spp(zp)	40	.07	abs	.03	22	.22	.09	.15
Synodontidae(pi)	32	abs	.11	.05	23	abs	.23	.11
Coris flavovittata(bc)	34	.03	.05	.04	25	<.06	.14	.10
Dendrochirus barberi(pi)	38	abs	.07	<.04	26	abs	.19	<.10
Adioryx spp(bc)	37	abs	.07	.04	28	<.01	.14	.08
Top 10 taxa		7.5	12.7	9.2		8.3	19.0	12.8
Top 20 taxa		8.3	15.3	11.3		9.1	21.8	15.0
Top 30 taxa		8.6	16.4	12.3		9.4	22.9	16.0
Total fishes		9.0	16.7	13.3		9.6	23.7	17.4

[a/] *Acanthurus nigrofuscus* and/or *A. nigroris*
[b/] *Scarus* spp adults, including *S. perspicillatus* and *S. sordidus*

Table 3.--FFS. Summary comparisons between July 1992 and September 1995 densities (N·10 m^{-2}), by habitat and across both major habitats, for major functional groupings of fishes. All tests were evaluated at $\alpha_{crit} < \alpha_{2,0.10/m}$ with m's as defined in the Methods. Standard errors are listed in parentheses for the July 1992 means. Sample sizes are 4, 5 and 9 for BR, PR, and both habitats, respectively. (* indicates significance at $< \alpha_{2,0.10/m}$.)

Trophic level/guild	Reef type	JUL 1992 mean (se)	% total fishes	Change (%)	Prob. change=0
Total fishes	BR	4.7 (1.3)	100	+ 37	0.001 *
	PR	18.1 (1.0)	100	+ 68	<0.001 *
	both	12.1 (2.5)	100	+ 63	<0.001 *
Herbivores	BR	1.6 (0.4)	34	+ 76	<0.001 *
	PR	7.5 (0.6)	41	+ 12	0.64
	both	4.8 (1.1)	40	+ 22	0.38
Secondary consumers	BR	3.2 (1.5)	66	+ 17	0.09
	PR	10.6 (0.4)	59	+ 107	<0.001 *
	both	7.3 (1.5)	60	+ 90	<0.001 *
benthic carnivores	BR	1.6 (0.3)	34	+ 6	0.68
	PR	6.0 (0.6)	33	+ 140	<0.001 *
	both	4.1 (0.9)	34	+ 117	<0.001 *
planktivores	BR	1.5 (1.3)	32	+ 22	0.41
	PR	4.1 (0.4)	23	+ 58	<0.001 *
	both	2.9 (0.7)	24	+ 51	<0.001 *
corallivores	BR	0.07(.03)	1	+ 43	0.35
	PR	0.14(.06)	1	+ 66	0.36
	both	0.11(.03)	1	+ 59	0.16
piscivores	BR	0.05(.02)	1	+ 149	0.61
	PR	0.28(.07)	>1	+ 140	0.026 *
	both	0.18(.05)	>1	+ 141	0.024 *

Table 4.--FFS and MWAY. Summary of nominal (signed) changes in density within the top 30 taxa of reef fishes, grouped by major trophic level and carnivore feeding guild, between the July 1992 (FFS) or August 1993 (MWAY) and the September 1995 surveys. Noted are results for binomial tests of the relative number of nominal increases and decreases.

	French Frigate Shoals		Midway Atoll	
	Increase	Decrease	Increase	Decrease
Herbivores	4	4	4	5
Secondary consumers	10	12	9	12
benthic carnivores	5	8	5	10
planktivores	3	2	4	1
corallivores	1	0	0	1
piscivores	1	2	--	--
Total fishes	14	16	13	17
	Ho : # decreases = # increases			
	H_{a2} : # decreases ≠ # increases			
	14/30 increases		13/30 increases	
	P=0.86		P=0.58	

Table 5.--MWAY. Summary comparisons between August 1993 and September 1995 densities ($N \cdot 10\ m^{-2}$), by habitat and across both major habitats, for major functional groupings of fishes. Sample sizes are 4, 5 and 9 for BR, PR, and both habitats, respectively. Other details are noted in Table 3 caption.

Trophic level/guild	Reef type	AUG 1993 mean (se)	% total fishes	Change (%)	Prob. change=0
Total fishes	BR	9.0 (1.2)	100	+ 7	0.75
	PR	16.7 (1.8)	100	+ 42	0.32
	both	13.3 (1.7)	100	+ 31	0.29
Herbivores	BR	3.8 (0.7)	42	+ 51	0.60
	PR	5.0 (0.5)	30	- 27	0.12
	both	4.5 (0.5)	34	+ 3	0.97
Secondary consumers	BR	5.2 (0.7)	58	- 25	0.65
	PR	11.7 (1.6)	70	+ 67	0.13
	both	8.8 (1.4)	66	+ 46	0.28
benthic carnivores	BR	4.1 (0.5)	46	- 57	<.001 *
	PR	6.0 (0.9)	36	+ 59	0.15
	both	5.1 (0.6)	38	+ 18	0.65
planktivores	BR	0.8 (0.5)	11	+ 150	0.61
	PR	5.3 (1.1)	32	+ 85	0.41
	both	3.3 (1.0)	25	+ 92	0.16
corallivores	BR	0.11 (.03)	1	- 57	0.99
	PR	0.09 (.05)	<1	+ 30	0.58
	both	0.18 (.05)	>1	- 32	0.29
piscivores	BR	<0.01 (<.01)	<1	+ 300	0.35
	PR	0.22 (.10)	>1	+ 82	0.69
	both	0.12 (.07)	1	+ 84	0.65

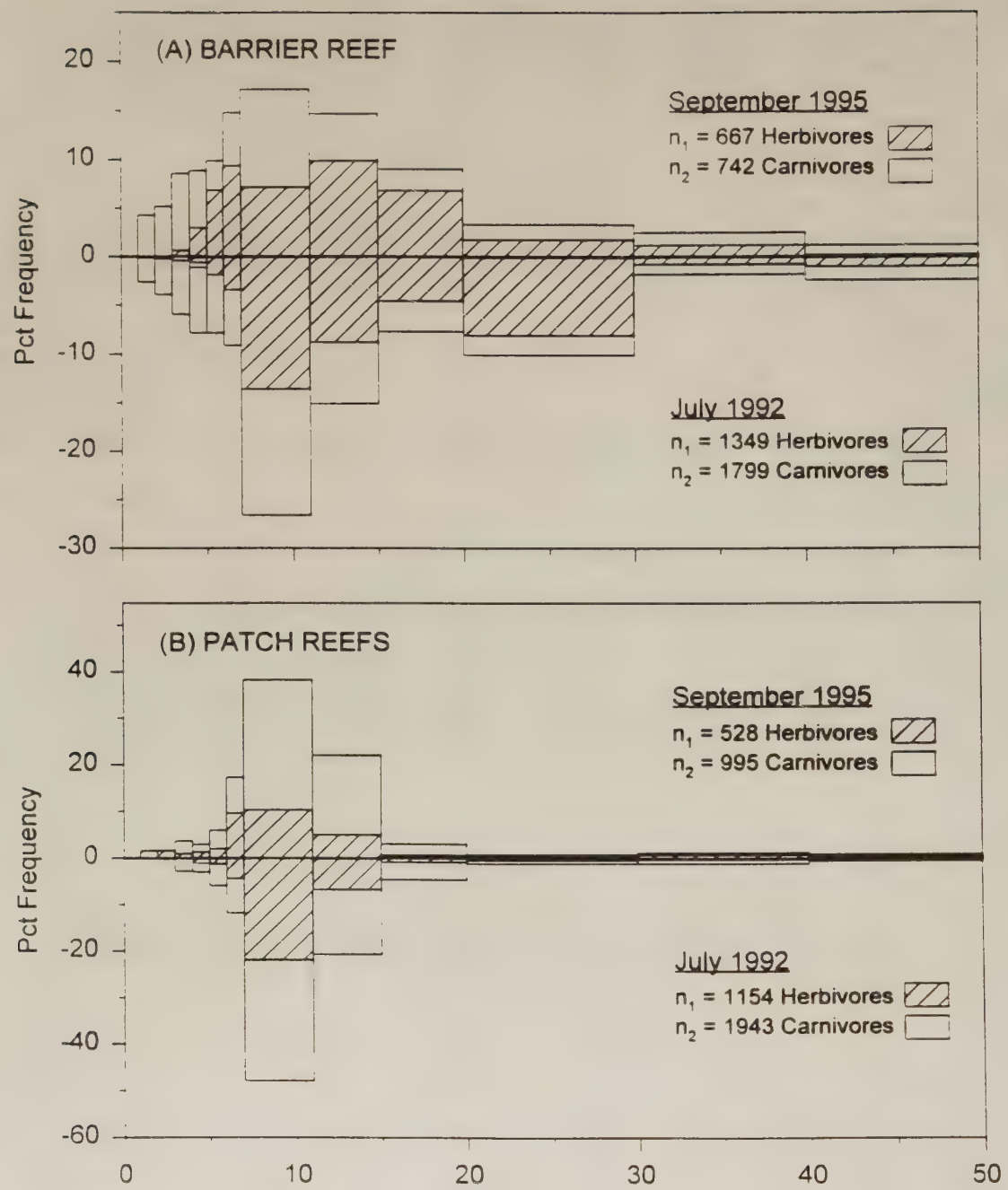

Figure 1--FFS. Percentage frequency distributions of body length classes (cm SL) for herbivores (diagonal-right histograms) and carnivores (hollow histograms). Data for the barrier reef and patch reefs are plotted in panels A and B, respectively. In each panel, data for the September 1995 and July 1992 surveys are plotted above and below the horizontal axis, respectively.

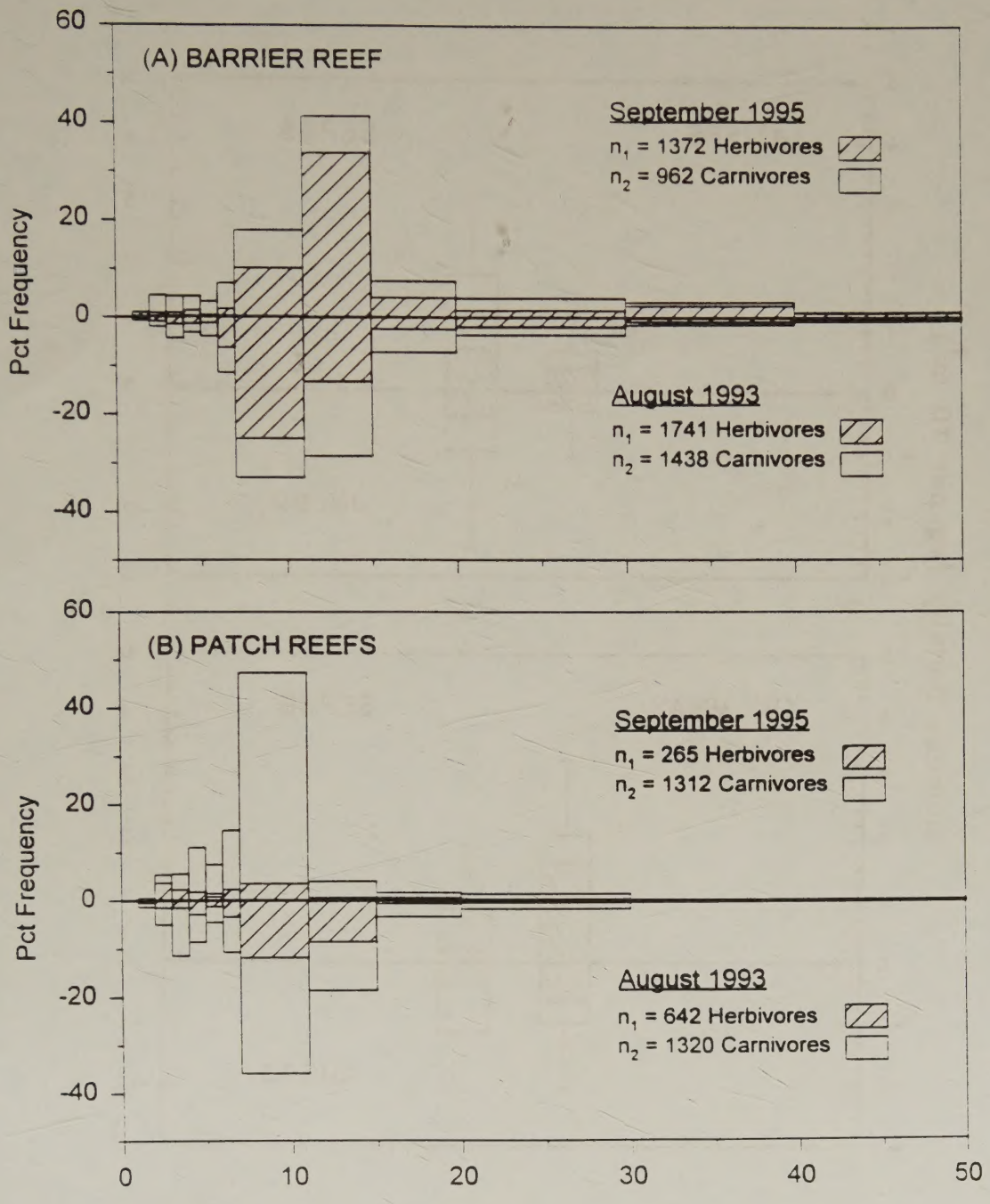

Figure 2--MWAY. Percentage frequency distributions of body length classes (cm SL) for herbivores and carnivores on the barrier reef (Panel A) and patch reefs (B), during the September 1995 (above x-axis) and August 1993 (below x-axis) surveys.

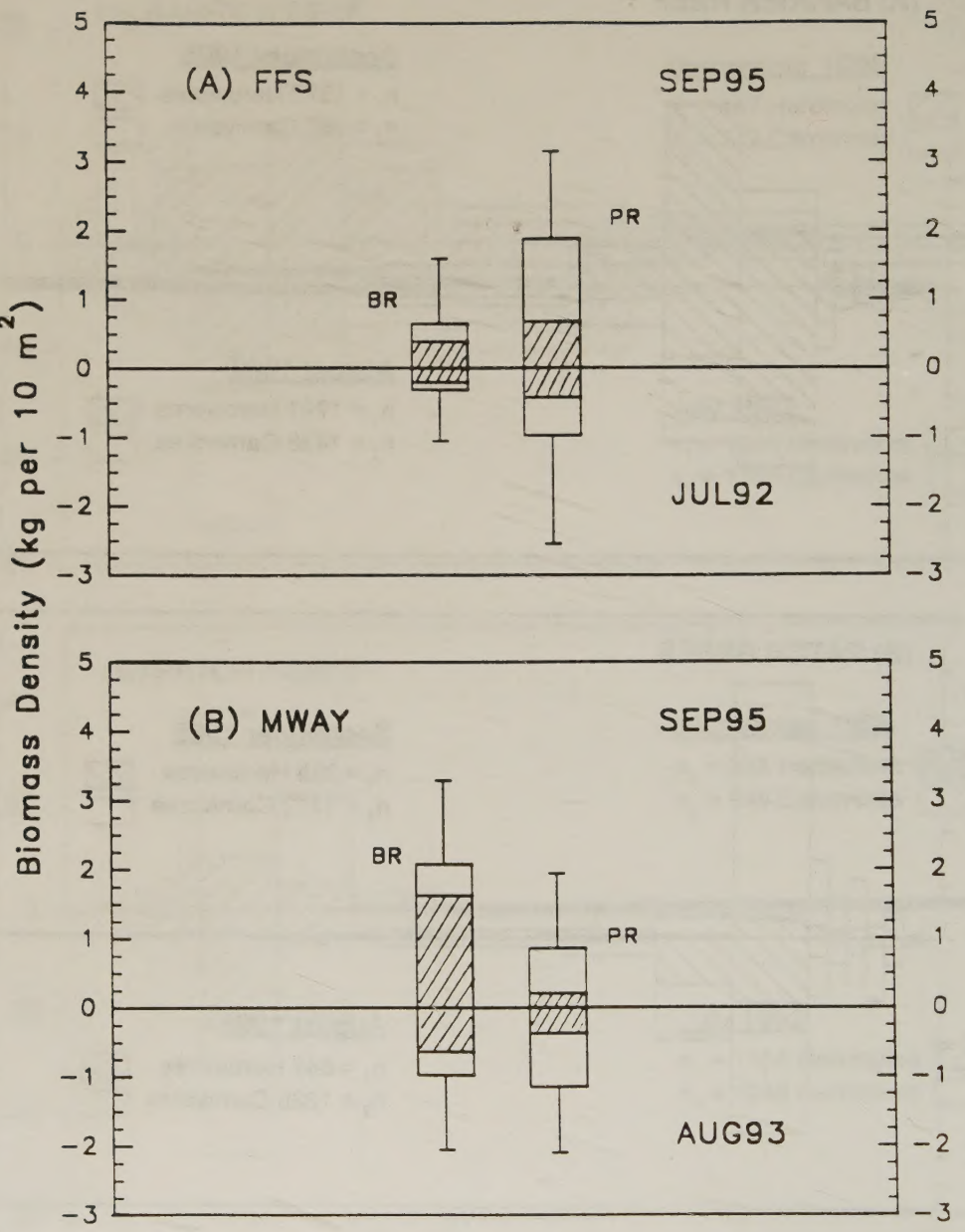

Figure 3--(A) FFS and (B) MWAY. Estimated biomass densities ($kg \cdot 10\ m^{-2}$) of herbivores (diagonal-right histograms) and carnivores (hollow histograms), during surveys in September 1995 (above x-axis) and in July 1992 at FFS or in August 1993 at MWAY (below x-axis). Also indicated is one approximate standard error of the biomass density of total (herbivore plus carnivore) fishes in each habitat during each survey.